Effectiveness of water-saving technologies for the restoration of endemic *Opuntia* cacti in the Galápagos Islands, Ecuador

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Restoration of keystone species is a primary strategy used to combat biodiversity loss and recover ecological services. This is particularly true for oceanic islands, which despite their small land mass, host a large fraction of the planet's imperiled species. The endemic Opuntia spp. cacti are one example and a major focus for restoration in the Galápagos archipelago, Ecuador. These cacti are keystone species that support much of the unique vertebrate animal community in arid zones, yet human activities have substantially reduced Opuntia populations. Extreme aridity poses a major obstacle for restoring Opuntia populations yet water-saving technologies may aid restoration efforts. The aim of this study was to evaluate current restoration efforts and the utility of two water-saving technologies as tools for restoring Opuntia populations in the Galápagos archipelago. We planted 1425 seedlings between 2013 and 2018, of which 66% had survived by the end of 2018. Compared with no-technology controls, seedlings planted with Groasis Waterboxx® water-saving technology (polypropylene trays with water reservoir and protective refuge for germinants) had increased survival on one island (Plaza Sur) and growth rate on four islands whereas the "Cocoon" water-saving technology (similar technology but made of biodegradable fiber) did not affect growth and actually reduced seedling survival. Survival and growth rate were also influenced by vegetation zone, altitude, and precipitation in ways largely contingent on island. Overall, our findings suggest that water-saving technologies are not always universally applicable but can substantially increase the survival and growth rate of seedlings in certain conditions, providing in some circumstances a useful tool for improving restoration outcomes for rare plants of arid ecosystems.

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Abstract

Restoration of keystone species is a primary strategy used to combat biodiversity loss and recover ecological services. This is particularly true for oceanic islands, which despite their small land mass, host a large fraction of the planet's imperiled species. The endemic *Opuntia* spp. cacti are one example and a major focus for restoration in the Galápagos archipelago, Ecuador. These cacti are keystone species that support much of the unique vertebrate animal community in arid zones, yet human activities have substantially reduced *Opuntia* populations. Extreme aridity poses a major obstacle for restoring *Opuntia* populations yet water-saving technologies may aid restoration efforts. The aim of this study was to evaluate current restoration efforts and the utility of two water-saving technologies as tools for restoring *Opuntia* populations in the Galápagos archipelago. We planted 1425 seedlings between 2013 and 2018, of which 66% had survived by the end of 2018. Compared with no-technology controls, seedlings planted with Groasis Waterboxx® water-saving technology (polypropylene trays with water reservoir and protective refuge for germinants) had increased survival on one island (Plaza Sur) and growth rate on four islands whereas the “Cocoon” water-saving technology (similar technology but made of biodegradable fiber) did not affect growth and actually reduced seedling survival. Survival and growth rate were also influenced by vegetation zone, altitude, and precipitation in ways largely contingent on island. Overall, our findings suggest that water-saving technologies are not always universally applicable but can substantially increase the survival and growth rate of seedlings in certain conditions, providing in some circumstances a useful tool for improving restoration outcomes for rare plants of arid ecosystems.

Introduction

The restoration of previously abundant keystone species is one way to combat loss of biodiversity and ecological services (Grime, 1998). This is particularly true on oceanic islands, which comprise little of the planet’s land mass yet host a disproportionate amount of its imperiled species (Myers et al., 2000; Campbell & Donlan, 2005). The Galápagos archipelago is a case in point: its land area is minimal (8006 km^2) yet it hosts a remarkable array of endemic life forms with as many as 60% of its 168 endemic plant species now threatened with extinction (Tye, 2007; Black, 1973). Active restoration programs are underway throughout the archipelago. For example, Project Isabela (1997-2006), was the world’s largest restoration effort at the time and dedicated to eradicating introduced mammal herbivores on multiple islands in the archipelago (Carrion et al., 2011).

The *Opuntia* spp. cacti (prickly pear cactus) are a major focus for restoration in the Galápagos archipelago, Ecuador, which hosts six endemic species, with 14 total taxa when including varieties. Human impact in the Galápagos archipelago has steadily increased over the last 200 years (Jaramillo, 1998), resulting in declines of *Opuntia* populations on these islands (Snell, Snell & Stone, 1994). Several factors have been attributed as the primary threats to Opuntias including herbivory by introduced mammals (Snell, Snell & Stone, 1994), extinction of keystone predators that once regulated numbers of cactivores (Sulloway & Noonan, 2015), and the increased intensity of El Niño events (Snell, Snell & Stone, 1994; Hicks & Mauchamp, 1996). *Opuntia* cacti provide many ecosystem services for other native and endemic species (Grant & Grant, 1981; Hicks & Mauchamp, 1995, 1996; Gibbs, Marquez & Sterling, 2008). Examples include Galápagos giant tortoises and land iguanas that depend on *Opuntia* cacti as a food source while also contributing to *Opuntia* regeneration through seed dispersal (Hamann, 1993; Snell, Snell & Stone, 1994; Gibbs, Marquez & Sterling, 2008; Gibbs, Sterling & Zabala, 2010). Efforts are being made to protect and restore populations of these imperiled cacti (Hicks & Mauchamp, 1996) but it is not clear which factors most control *Opuntia* populations (Sulloway & Noonan, 2015). *Opuntia* declines on Plaza Sur Island, for example, are especially pronounced and regeneration remains low despite goat eradication in the 1960s (Snell, Snell & Stone, 1994). Nonetheless, active planting of these species is critical for preventing extinction until their threats are better understood and eliminated.

Severe aridity poses a major obstacle for restoring plant communities over much of Galápagos, including the restoration of xerophytes such as cacti. The lowland zones of the archipelago, where Opuntias are most common and historically abundant (Browne et al., 2003), can receive less than 10 cm rainfall annually (Trueman & d'Ozouville, 2010). "Water-saving" technologies are tools that may help increase survival and growth of planted cactus seedlings while reducing the need for manual watering in these arid environments of the Galápagos (Jaramillo, 2015; Jaramillo, Cueva, Jiménez, & Ortiz, 2014; Jaramillo et al., 2015; Hoff, 2014; Jaramillo, Tapia, & Gibbs, 2018; Peyrusson, 2018, Faruqi et al., 2018; Kulkarni, 2011). Although these technologies show much promise, there remains a dearth in formal scientific studies evaluating their efficacy (but see Liu, Li, & Ren, 2014). Therefore, the objective of the current study was to determine the success of current restoration efforts and evaluate the utility of two water-saving technologies as tools for restoring *Opuntia* populations in the Galápagos archipelago. Through this objective we hope to better understand the utility of water-saving technologies for restoring these and other keystone plant species in arid island ecosystems throughout the world.

Materials & Methods

Study Area, Focal Species, and Water-saving Technologies

The Galápagos archipelago is located in the Pacific Ocean, about 1000 km west of the coast of mainland Ecuador (1°39' N, 92°0' W to 1°26' S, 89°14' W, WGS 84, Fig. 1) (DPNG, 2014). Our study focused on measuring the utility of water-saving technologies for enhancing cactus growth and survival of four endemic *Opuntia* taxa within the archipelago: *Opuntia echios* var. *echios* Howell, *Opuntia echios* var. *gigantea* Howell, *Opuntia megasperma* var. *megasperma* Howell, and *Opuntia megasperma* var. *orientalis* Howell (Hicks & Mauchamp, 1996). The water-saving technologies used in this study function by sheltering seedlings and ground around them from the heat of the sun while storing and providing water. We evaluated two technologies: Groasis Waterboxx® (Groasis), a protective polypropylene box that collects rainwater that it provides to the plant (Hoff, 2014); and the Cocoon system, a 99% biodegradable box that contains and provides water to the plant similar to Groasis, but Cocoon is only filled with water at the time of planting (Land Life Company, 2015; Faruqi et al., 2018). These water-saving technologies have been proposed as a tool to assist plant restoration of *Opuntia* taxa via "Galápagos Verde 2050" (GV2050), a project started by the Charles Darwin Foundation in 2013 with the mission of restoring degraded ecosystems and aiding with sustainable agriculture in the Galápagos archipelago (Jaramillo et al., 2014, 2015, 2017). GV2050 seeks to restore ecosystems by using a data-informed experimental approach for understanding the best conditions, mechanisms, and tools for successful plantings of native and endemic species (Jaramillo et al., 2015).

Planting and Data Collection

A total of 1425 total cacti (1137 *Opuntia echios* var. *echios*, 68 *Opuntia echios* var. *gigantea*, 24 *Opuntia megasperma* var. *megasperma*, and 196 *Opuntia megasperma* var. *orientalis*) were planted on six islands (Baltra, Española, Floreana, Plaza Sur, San Cristóbal, and Santa Cruz) between 2013 and 2018 (Table 1). Permission to plant Opuntias within protected sites on these islands was granted by the Dirección del Parque Nacional Galápagos (DPNG) through permit number PC-11-19 (Table 2). To evaluate the factors most important for successful *Opuntia* restoration data were used only from Opunitas that were grown from seed and planted using either Groasis, Cocoon, or control (no technology) treatments on Floreana, Santa Cruz, Baltra, and Plaza Sur islands yielding a sample of 1029 *Opuntia* individuals of three taxa (Table 1).

Planting sites on each island were selected based on locations where historic *Opuntia* populations were known to have thrived but are now in decline (Sulloway & Noonan 2015; Sulloway et al., 2013; Table 2). Seedlings were sown from seeds collected in each respective planting location using standardized seed collection and stratification techniques and grown for one year at the Charles Darwin Research Station, Santa Cruz Island, before transferring to each island (Jaramillo, 2019; Jaramillo, Tapia & Gibbs, 2017). Each seedling was randomly assigned a treatment of either control (no technology), Groasis, or Cocoon, ensuring a representative sample of replicates within each treatment and site. The number of controls was maintained at one control for every five Groasis or Cocoon technology treatment replicates. Plantings were conducted according to established methods for installing Groasis, Cocoon, and controls (Jaramillo et al., 2017). Wire fences were secured and maintained around each individual planting on Plaza Sur and Baltra islands to prevent land iguana herbivory. Planting site co-variates were recorded at time of planting: altitude (elevation), soil type (rocky sand, rocky clay, rich clay, and rich sandy clay), vegetation zone (arid, littoral, and transitional; Johnson & Raven, 1973), and treatment (control, Groasis, and Cocoon). Growth (vegetative height) and qualitative plant state ("good," "regular," "poor," and dead) were noted during each repeated visit approximately every six weeks following planting.

Two measures were used to evaluate restoration success (Menendez & Jaramillo, 2015). Two-year survival was quantified as whether or not a seedling survived for at least two years after planting—the period of greatest mortality risk. Only seedlings planted before 2017 (at least two years since planting) were included in that analysis. Relative growth rate was also calculated based on the vegetative height of each seedling over time. Whereas survival is the primary metric for establishing success of population restoration, growth rate can indicate the speed of ecosystem recovery due to the rate of increase in the biomass of a keystone species (Grime, 1998). An additional environmental covariate of total precipitation across the six months following planting was compiled based on available climate data from 2013 to 2018 (Trueman & D'Ozouville, 2010; CDF, 2018).

Data analysis

All statistical analyses were conducted using the R statistical software package v3.3.3 (R Core Team, 2017). To test the overall effect of water-saving technologies on the restoration of

Opuntia cacti, a model comparison approach was implemented using fixed- and mixed-effects regression models of the form:

2-year survival logistic fixed-effect model:

$$2YearSurvival = \alpha + \beta_1 \times \ treatment + \ \beta_2 \times \ 6MonthPrecip + \ \beta_3 \times \ Zone + \ \beta_4 \times \ Altitude + \ \beta_5 \times \ island$$

Relative growth rate linear mixed-effect model:

$$\log(RGR) = \alpha + \beta_1 \times \ treatment + \ \beta_2 \times \ 6MonthPrecip + \ \beta_3 \times \ SoilType + \ \beta_4 \times \ Zone + \beta_5 \times \ Altitude + \ \beta_6 \times \ PlantAge + \ \beta_6 \times \ island + N(0, {\sigma^2}_{PlantID})$$

The growth rate model is a general linear mixed-effects regression fit using the 'lme4' package (Bates et al., 2015). Relative growth rate (RGR) was calculated as the relative rate of increase in height over time and was log-transformed after adding one to meet assumptions of normality. Plant age was included in the model to account for the fact that RGR changes as seedlings get older. Plant ID is included as a random effect. Random effects account for within-group correlation that results from non-independent data points (Pinheiro & Bates, 2000). For example, our growth data are based on repeated measures of each individual plant, which means that growth measurements are not independent within an individual plant. The random effect for Plant ID allows us to include all observations in our analysis by accounting for this non-independence. The two-year survival model tested the overall survival of each seedlings two years after planting and was fit using a generalized linear model function with a binomial family logit function in the 'base' package (R Core Team, 2017). Because only one data point was available for each plant, the lower sample size required a simpler model in which soil type was removed in order to allow the model to converge successfully and no random effects were necessary. These models were then compared to null models using the likelihood-ratio to test for the effect of treatment on growth rate and survival. Null models were the same as the models listed above except for the exclusion of technology treatment. A significant difference between the two models indicates that the variable that was excluded (i.e., treatment) is a significantly important predictor.

We examined the relative effect of each variable within the growth rate and survival models to assess the relative importance of technologies as well as other environmental factors such as soil type and altitude. All continuous variables in our models were standardized by subtracting the mean and dividing by two times the standard deviation in order to relativize the effect of each variable coefficient on growth rate and two-year survival (Gelman, 2008). Confidence intervals (95%) for each coefficient in each full model were then bootstrapped using the 'boot' package in R (Canty, 2017) and plotted for visual comparison. P-values were generated using the Satterthwaite method in the 'lmerTest' package in R (Kuznetsova et al., 2017). P-values generated from mixed-effect models are not always accurate, but we include these values for the sake of highlighting the degree to which variables differ in their relative importance. Furthermore, all significance values generated in this way were consistent with bootstrapped confidence interval results. Coefficients for logistic models were back-transformed to odds ratio by exponentiating and subtracting one. In this way the coefficient values can be interpreted as the proportional effect of each variable on increasing (or decreasing if negative) the probability of two-year survival. Each model was fit using data from all four islands included in the analysis (Baltra, Floreana, Santa Cruz, and Plaza Sur), but due to high control treatment mortality on Plaza Sur, the models were also tested using data that *excluded* Plaza Sur as well as using data *exclusively from* Plaza Sur. When testing with data exclusively from Plaza Sur, "island" was removed from the models and treatment type consisted of only Groasis and controls because no Cocoons were used on Plaza Sur. Finally, the current state of all planted individuals included in the analysis (up through 2018) was plotted as stacked bar plots to visualize rates of survival between islands and treatments.

Results

General outcomes

Of the 1425 *Opuntia* spp. individuals planted between 2013 and 2018, (most plantings were made in 2015 and 2016, Fig. 2), 943 Opuntias remained alive by the end of 2018 (66% overall survival, Fig. 2). On Plaza Sur, 737 *Opuntia* individuals were planted between 2015 and 2018 with 452 survivors by the end of 2018 (an increase of 135% from the last recorded population estimates of 334 in 2014; Fig. 3). Survival of seedling plantings on Plaza Sur was 26.8% (n = 82) for controls and 62.2% (*n* = 519) for Groasis (Fig. 4a). Survival of seedling plantings on Floreana was 66.7% (*n* = 3) for controls and 31.2% (*n* = 16) for Groasis (Fig. 4b). Survival of seedling plantings on Baltra was 79.7% (*n* = 74) for controls, 45% (*n* = 20) for Cocoon, and 65.5% (*n* = 255) for Groasis (Fig. 4c). Survival of seedlings planted on Santa Cruz was 77.8% (*n* = 9) for controls, 27.8% (*n* = 18) for Cocoon, and 72.7% (*n* = 33) for Groasis (Fig. 4d).

Outcomes across all islands

Model comparisons: Treatment type (Groasis, Cocoon, or Control) was associated with growth rate of *Opuntia* species (χ^2 (2) = 60.77, P < 0.001) and two-year survival rate of *Opuntia* seedlings (χ^2 (2) = 154.73, P < 0.001). In the two-year survival logistic regression, altitude (1.14, P < 0.001), littoral zone (14.91, P < 0.001), transitional zone (13.17, P = 0.035), and six-month precipitation (-0.38, P = 0.004) had odds ratios with confidence intervals that did not overlap zero (Fig. 5a). Groasis technology had a positive odds ratio of 0.73 (P < 0.001), while Cocoon had a negative odds ratio of -0.95 (P < 0.001) (Fig. 5a). In the growth rate regression, littoral zone (0.48, P < 0.001), plant age (-0.53, P < 0.001), and six-month precipitation (0.25, P = 0.031) all had effect sizes with confidence intervals that did not overlap zero (Fig. 5b). Groasis technology had a positive effect size with a coefficient of 0.54 (P < 0.001), while Cocoon had an insignificant coefficient (P = 0.160) (Fig. 5b).

Outcomes on Plaza Sur Island only

Model comparisons: On Plaza Sur Island, treatment type (Groasis or Control) was associated with growth rate of *Opuntia* species (χ^2 (1) = 18.92, P = 0.001) and two-year survival rate of *Opuntia* seedlings (χ^2 (1) = 57.93, P < 0.001). In the two-year survival logistic regression, littoral zone (310.5, P < 0.001), altitude (1.32, P < 0.001), and six-month precipitation (-0.62, P < 0.001) had odds ratios with confidence intervals that did not overlap zero (Fig. 5c). Groasis technology had a positive odds ratio of 3.19 (P < 0.001) (Fig. 5c). In the growth rate regression, littoral zone (0.49, P < 0.001), plant age (-0.3, P < 0.001), six-month precipitation (-0.22, P = 0.001), and altitude (0.18, P = 0.012) all had effect sizes with confidence intervals that did not overlap zero (Fig. 5d). Groasis technology had a positive effect size with a coefficient of 0.46 (P < 0.001) (Fig. 5d).

Outcomes on all islands excluding Plaza Sur

Model comparisons: Treatment type (Groasis, Cocoon, or Control) was associated with growth rate of *Opuntia* species (χ^2 (2) = 23.62, P < 0.001), but not with two-year survival rate of *Opuntia* seedlings (χ^2 (2) = 43.31, P > 0.001). In the two-year survival logistic regression, transition zone (-0.99, P < 0.001) had a negative odds ratio with confidence intervals that did not overlap zero (Fig. 5e). Both Groasis and Cocoon technologies had significant negative odds ratios of -0.31 (P = 0.034) and -0.9 (P > 0.001) respectively (Fig. 5e). In the growth rate regression, plant age (-0.78, P < 0.001) and six-month precipitation (0.51, P < 0.001) had effect sizes with confidence intervals that did not overlap zero (Fig. 5f). Groasis technology had a positive effect size with a coefficient of 0.45 (P < 0.001), while cocoon had an insignificant coefficient (P > 0.05) (Fig. 5f).

Discussion

Water-saving technologies enhanced survival and growth of *Opuntia* plantings, but benefits of these technologies were highly contingent upon planting environment. For example, Groasis technology was effective at increasing growth rate across islands overall, but was only effective at aiding survival on Plaza Sur Island where Groasis increased the probability of two-year survival of seedlings more than three-fold (319%) (Fig. 5). Cocoon technology, however, provided no improvement in growth rate and actually reduced probability of two-year survival of seedlings by 95% overall (Fig. 5). Altogether, our *Opuntia* restoration efforts have increased the population of *Opuntia* spp. in the Galápagos archipelago by 943 individuals (66% survival of 1425 plantings), more than doubling the population of *Opuntia* cacti on Plaza Sur Island, from 334 to 786 in just four years (Fig. 3).

These results emphasize the species- and site-specific contingencies of applying water-saving technologies for plant restorations. For example, Cocoon technology did not provide any advantage when planting Opuntias in the Galápagos archipelago. This is despite the fact that in other systems and with other species Cocoon has been shown to increase survival rates in planted trees from 0-20% to 75-95% (Faruqi et al., 2018). One possible explanation is that *Opuntia* cacti have a short initial rooting depth compared to other species (Snyman, 2005), and this may reduce access to the water available from the Cocoon (Land Life Company, 2015). *Acacia macracantha*, for example, has much deeper roots and has had much greater success when planted with Cocoon technology in the Galápagos (GV2050, *unpublished data*).

Although Groasis technology helped increase growth rate of Opuntias overall, it had a clear, positive effect on the survival of Opuntias only on Plaza Sur Island. A likely factor contributing to this is that compared to other islands, the majority of Opuntias were planted on Plaza Sur preceding the greatest period of drought in the Galápagos over the last five years (Appendix 1; CDF, 2018). Despite fairly regular seasonal patterns of water availability in the Galápagos (Snell & Rea, 1999; Restrepo et al., 2012), there remains much variability, especially that caused by El Niño events (Trueman & d'Ozouville, 2010). In this way Groasis may have the greatest advantage when ensuring water availability for Opuntias during periods of especially severe drought. *Opuntia* cacti are typically more resistant to desiccation and water stress compared to other species that do not have physiological adaptations for surviving low-water desert conditions (Racine & Downhower, 1974; Dubrovsky, 1998), and this may explain why Groasis was only effective for *Opunita* cacti under extreme drought. These findings support the idea that water availability for Opuntias plays less of a role in survival than previously assumed (Coronel, 2002; Jaramillo, Tapia & Gibbs, 2018; Racine & Downhower, 1974). This does not negate the value of the Cocoon or Groasis technology for restoration overall, but rather presents the important observation that water-saving technologies such as Cocoon and Groasis should be considered on a case-by-case basis and tested with each species and in different environmental conditions before making expansive planting efforts. Groasis technology may provide a form of insurance for the unpredictability of extreme drought events and the benefits of using Groasis technology may in some cases outweigh the costs in the long run.

Site co-variates also affected *Opuntia* survival and growth. In particular, vegetation zone, altitude, and precipitation were important predictors of *Opuntia* survival and growth but as with water-saving technologies, these effects were highly contingent on island. Opuntias had a greater survival and growth rate in the littoral vegetation zone on Plaza Sur but had greater survival in the arid vegetation zone on other islands. This effect may be due to an interaction between environmental and biotic factors unique to Plaza Sur or other islands. For example, Plaza Sur has especially high land iguana densities speculated to be due to the loss of its main predator from the island, the Galápagos hawk (Sulloway & Noonan, 2015). This high herbivore density may help keep invasive plant species in check on Plaza Sur—species that may otherwise shade out *Opuntia* seedlings on other islands (Schofield, 1973, Hicks & Mauchamp, 1996, 2000).

Surprisingly, six-month precipitation did not have a positive effect on seedling survival in any of our analyses, and actually decreased survival of seedlings planted on Plaza Sur. This finding contradicts conclusions from previous work by Coronel (2002) who found that precipitation during the six months following planting was an important factor for *Opuntia* survival. Coronel (2002), however, found that the negative effect of desiccation was mostly evident in Opuntias grown from cladodes rather than seeds as in the current analysis. Furthermore, most seedlings were planted on Plaza Sur at the start of a long period of drought so there was not as much variation in precipitation on Plaza Sur seedlings to fully test its effects. Altitude was only a significant predictor of survival and growth rate on Plaza Sur (Fig. 5). This may be in part because altitude is closely associated with vegetation zone, and this can account for some of the altitude effect. That said, it is not clear what is driving the positive effect of altitude on Plaza Sur. Although littoral zone has a positive impact on survival and growth, seedlings that are too low in elevation are more exposed to ocean salt spray which can increase seedling mortality (Boyce, 1954). Soil type had no significant effects on growth rate (Fig. 5), suggesting that, at least for Opuntias, substrate is of less importance for growth rate than factors such as vegetation zone or altitude. The effect of soil type on survival could not be tested with the current data due to limitations in sample size.

The observational aspects of our study have some inherent limits. Although it seems likely that extreme drought was the primary driver of control treatment seedling mortality on Plaza Sur, other effects cannot be ruled out. Plaza Sur is a small island (the smallest island by far of the four in this analysis: only 13 ha, with the next larger being Baltra at 2100 ha), which could increase the exposure of seedlings to salt spray, exposure to sea lion activity, as well as a suite of other effects associated with small islands (Lomolino & Weiser, 2001). It may also be that the high concentration of land iguanas and sea lions (Jaramillo pers. obs.) has impacted the edaphic environment of the island through their excrement as can be common on seabird islands (Rajakaruna et al., 2009). Thus, the small area and low variation in altitude, precipitation, and vegetation zones associated with Plaza Sur plantings suggests that any significant effect of these factors within Plaza Sur be taken cautiously when generalizing to *Opuntia* restoration beyond this island. The experimental treatments of the study involving water-saving technologies, however, do suggest that extreme drought is the most probable hypothesis for the high control mortality on Plaza Sur. Another important caveat is that taxon effects are confounded with island effects. With one exception, each island had a particular species or variety of *Opuntia* (Table 1). It is possible that some of the island-based differences are actually due to slightly different environmental requirements of the *Opuntia* taxa used in this study.

In conclusion, this study underlines the importance of considering the specific circumstances and methodologies that affect successful restoration. Water-saving technologies such as the Groasis Waterboxx® and Cocoon are promising systems for restoring species in arid environments but should not be assumed to function equally well in all environments and with all species. Even within one system, as in the current study, the benefits of Groasis vary tremendously and likely depend on the precipitation available following plantings. It is possible that species already adapted for low water conditions, such as cacti, have a much lower threshold at which Groasis or other water-saving technologies provide a benefit. Future evaluations of these technologies should monitor precipitation to test whether there is a threshold level of drought where these technologies become more effective. In some cases and for some species there may be no threshold for effective use as with the Cocoon technology for Opuntias. Preliminary plantings coupled with extensive environmental and experimental data collection is essential before large-scale planting efforts are initiated with water-saving technologies. The Galápagos Verde 2050 project of the Charles Darwin Foundation presents a model for data-informed adaptive management and conservation. We hope this model may inspire other restoration efforts to adopt similar data-informed approaches. Continued monitoring and accounting for context-specific contingencies in restoration work is essential (Cabin, 2007) and future restoration efforts should continually adapt management protocols based on current results (Parma et al., 1998).

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Table 1 (on next page)

Total number of *Opuntia* spp. individuals planted by island by Galápagos Verde 2050 (2013-2018).

Numbers in parentheses '()' are the number of individuals used in the current study analysis (Figures 4 & 5).

Table 1. Total number of *Opuntia* spp. individuals planted by island by Galápagos Verde 2050 (2013-2018). Numbers in parentheses '()' are the number of individuals used in the current study analysis (Figures 4 & 5).

Species	Baltra	Española	Floreana	Plaza Sur	San Cristóbal	Santa Cruz
Opuntia echios var. *echios*	400 (349)	—	—	737 (601)	—	—
Opuntia echios var. *gigantea*	—	—	—	—	—	68 (60)
Opuntia megasperma var. *megasperma*	—	—	20 (19)	—	4 (0)	—
Opuntia megasperma var. *orientalis*	—	196 (0)	—	—	—	—

Table 2(on next page)

List of all sites of Galápagos Verde 2050 *Opuntia* spp. restoration and number of *Opuntia* spp. individuals planted (2013-2018).

Numbers in parenthases ‘()’ represent the percent of individuals that have survived through 2018.

Table 2. List of all sites of Galápagos Verde 2050 *Opuntia* spp. restoration and number of *Opuntia* spp. individuals planted (2013-2018). Numbers in parenthases '()' represent the percent of individuals that have survived through 2018.

Island	Site Name	# Planted	UTM East[1]	UTM North[1]
Baltra (70%)	Antiguo basurero	158 (69%)	804668	9950436
	Casa de piedra	125 (74%)	802460	9948203
	Jardín ecológico Aeropuerto	1 (100%)	804100	9950795
	Parque Eólico	116 (68%)	803992	9950909
Española (79%)	Las Tunas	196 (79%)	199759*	9849118*
Floreana (40%)	Botadero de basura	3 (33%)	781054	9858587
	Cementerio	7 (29%)	780322	9858645
	Escuela Amazonas	5 (40%)	779594	9858865
	Gobierno Parroquial Floreana	1 (0%)	779530	9859029
	Oficina Técnica Parque Nacional Galápagos	4 (75%)	779531	9859244
Plaza Sur (61%)	Centro	254 (62%)	815800	9935365
	Los Lobos Este	253 (47%)	815936	815936
	Oeste Cerro Colorado	230 (76%)	815304	9935602
San Cristóbal (100%)	CA Jacinto Gordillo	4 (100%)	209711*	9900150*
Santa Cruz (65%)	Colegio Nacional Galápagos	2 (50%)	798782	9918296
	Espacio Verde ABG	8 (88%)	797864	9918887
	Fundación Charles Darwin	51 (67%)	800106	9917856
	Oficina Técnica Parque Nacional Galápagos	7 (29%)	799811	9917994

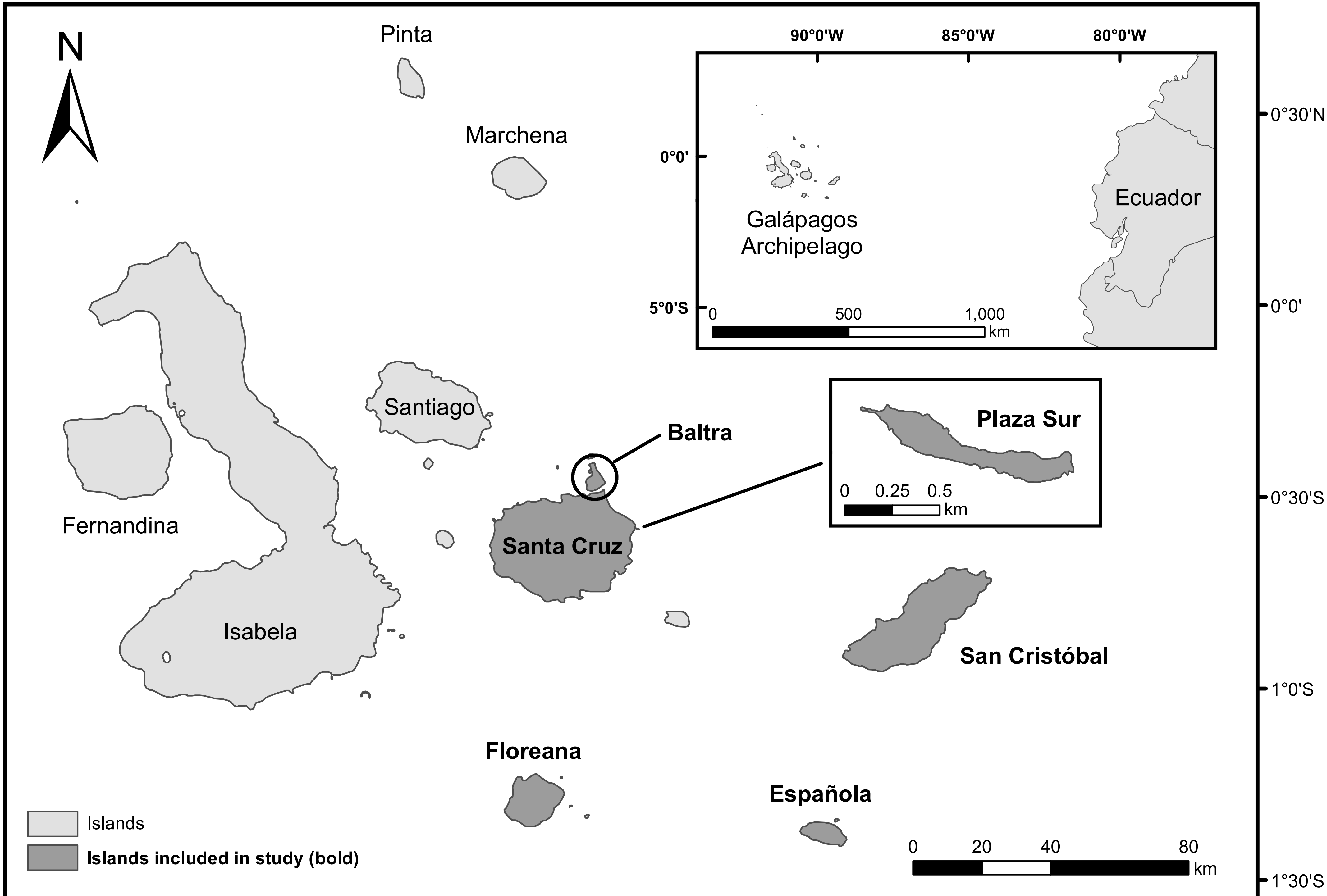
[1] UTM Zone = 15M, datum = WGS84

* UTM Zone = 16M

Figure 1 (on next page)

Map of the Galápagos Islands, Ecuador.

Islands included in the current study are darkened and labeled in bold.



N
Pinta
Marchena
Santiago
Baltra
Plaza Sur
0 0.25 0.5
km
Fernandina
Santa Cruz
Isabela
San Cristóbal
Floreana
Española
Islands
Islands included in study (bold)
0 20 40 80
km
90°0'W 85°0'W 80°0'W
0°0'
5°0'S
Galápagos Archipelago
Ecuador
0 500 1,000
km
0°30'N
0°0'
0°30'S
1°0'S
1°30'S
91°30'W 91°0'W 90°30'W 90°0'W 89°30'W 89°0'W

Figure 2 (on next page)

Total *Opuntia* spp. restoration from 2013 to 2018 across Baltra, Española, Floreana, Plaza Sur, San Cristóbal, and Santa Cruz islands.

Values above bars indicate total surviving individuals by the end of each year (y-axis values).

Values at the bottom indicate the total number of individuals planted each year.

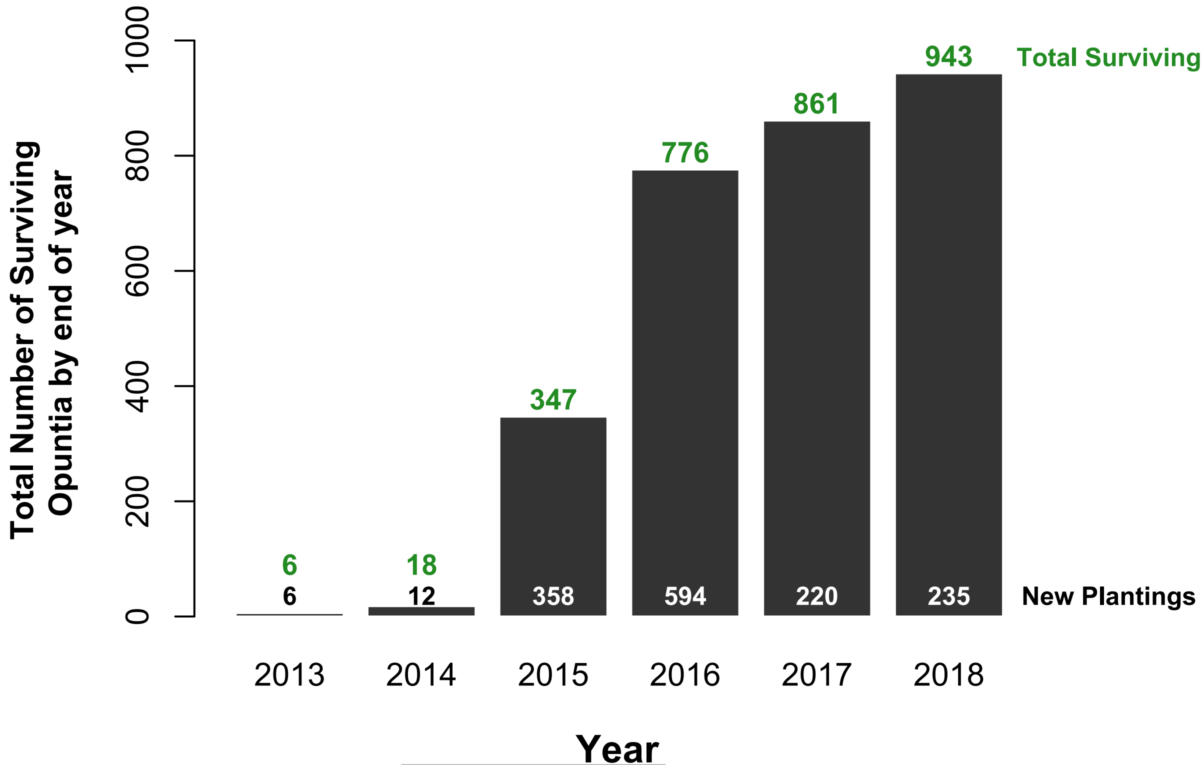

Total Number of Surviving
Opuntia by end of year
0
200
400
600
800
1000
6
18
347
776
861
943
Total Surviving
6
12
358
594
220
235
New Plantings
2013
2014
2015
2016
2017
2018
Year

Figure 3(on next page)

Approximate *Opuntia echios* var. *echios* population on Plaza Sur island from 1980 to 2018.

Redrawn from Snell et al. (1994) with 2014 addition from Sulloway and Noonan (2015), and 2015-2018 values based on estimate from 2014 (334) plus surviving individuals from Galápagos Verde 2050 (GV2050, green shading) replanting efforts.

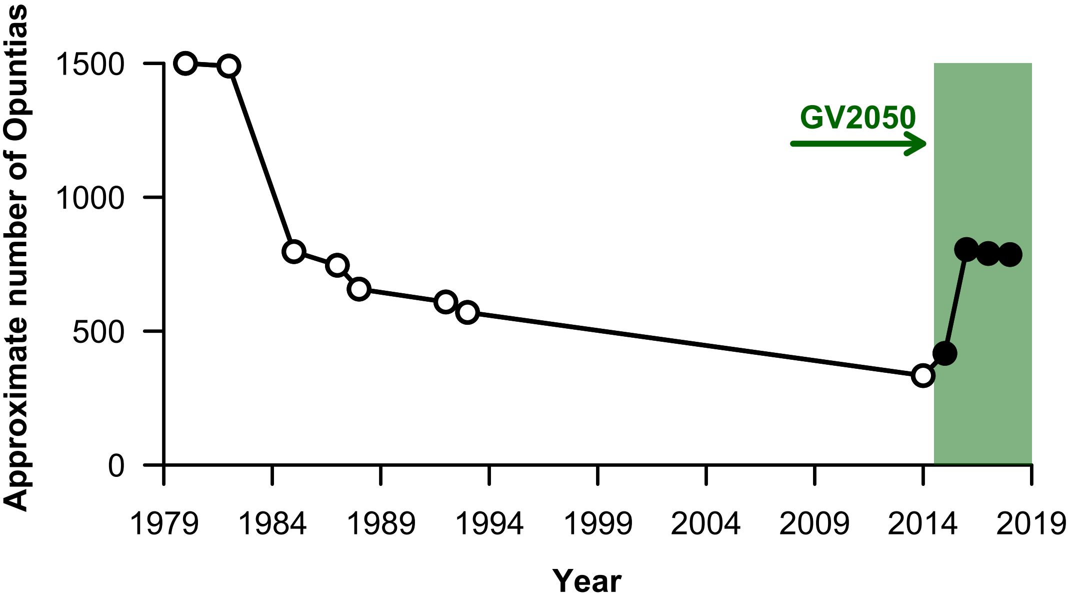

Approximate number of Opuntias
1500
1000
500
0
GV2050
1979
1984
1989
1994
1999
2004
2009
2014
2019
Year

Figure 4(on next page)

State of each planted *Opuntia* individual by the end of 2018 within each island.

A. Plaza Sur; B. Floreana; C. Baltra; D. Santa Cruz. “N” indicates the total number of individuals within each treatment on each island. Figure based on only those data used in the current analysis.

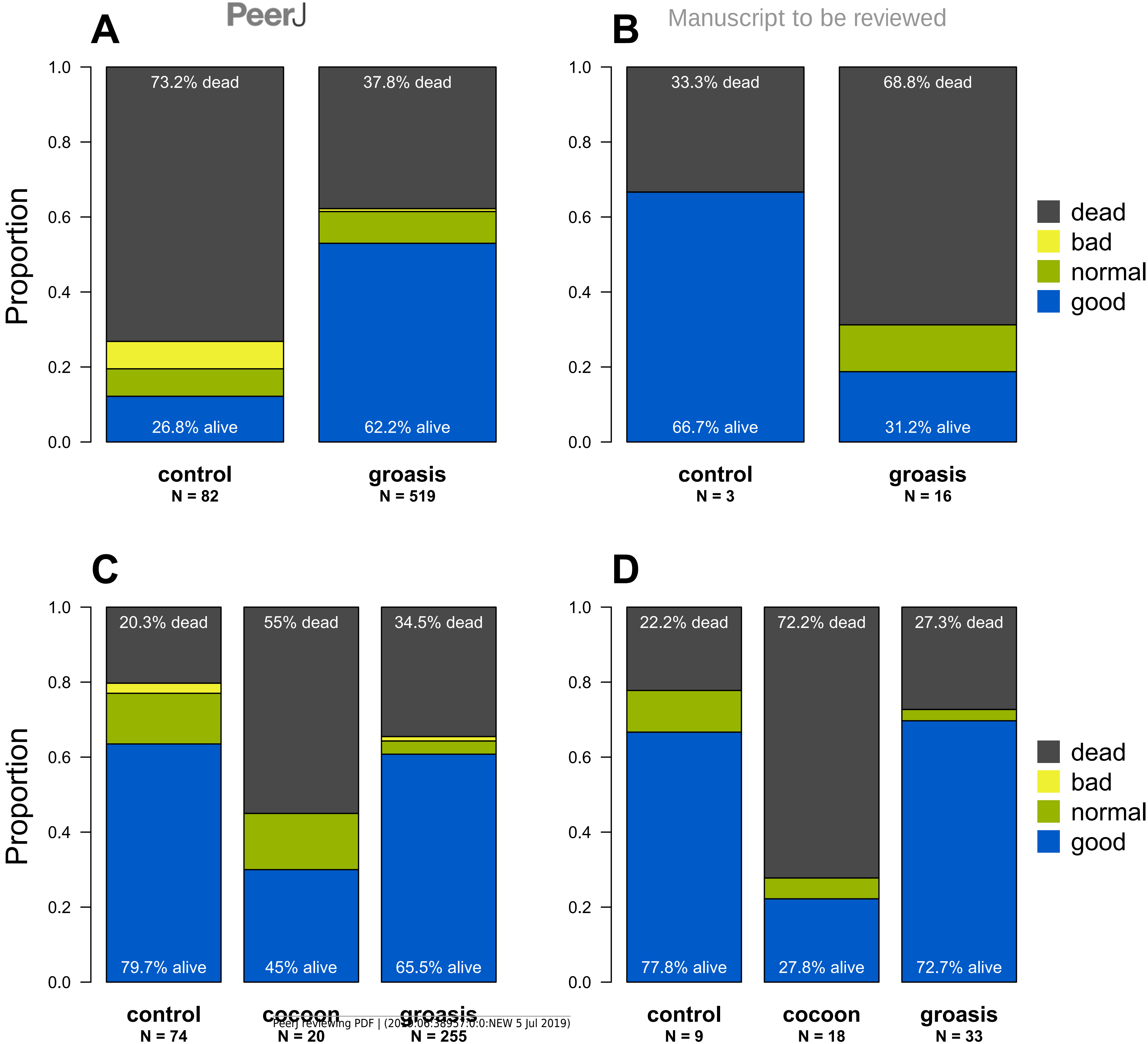
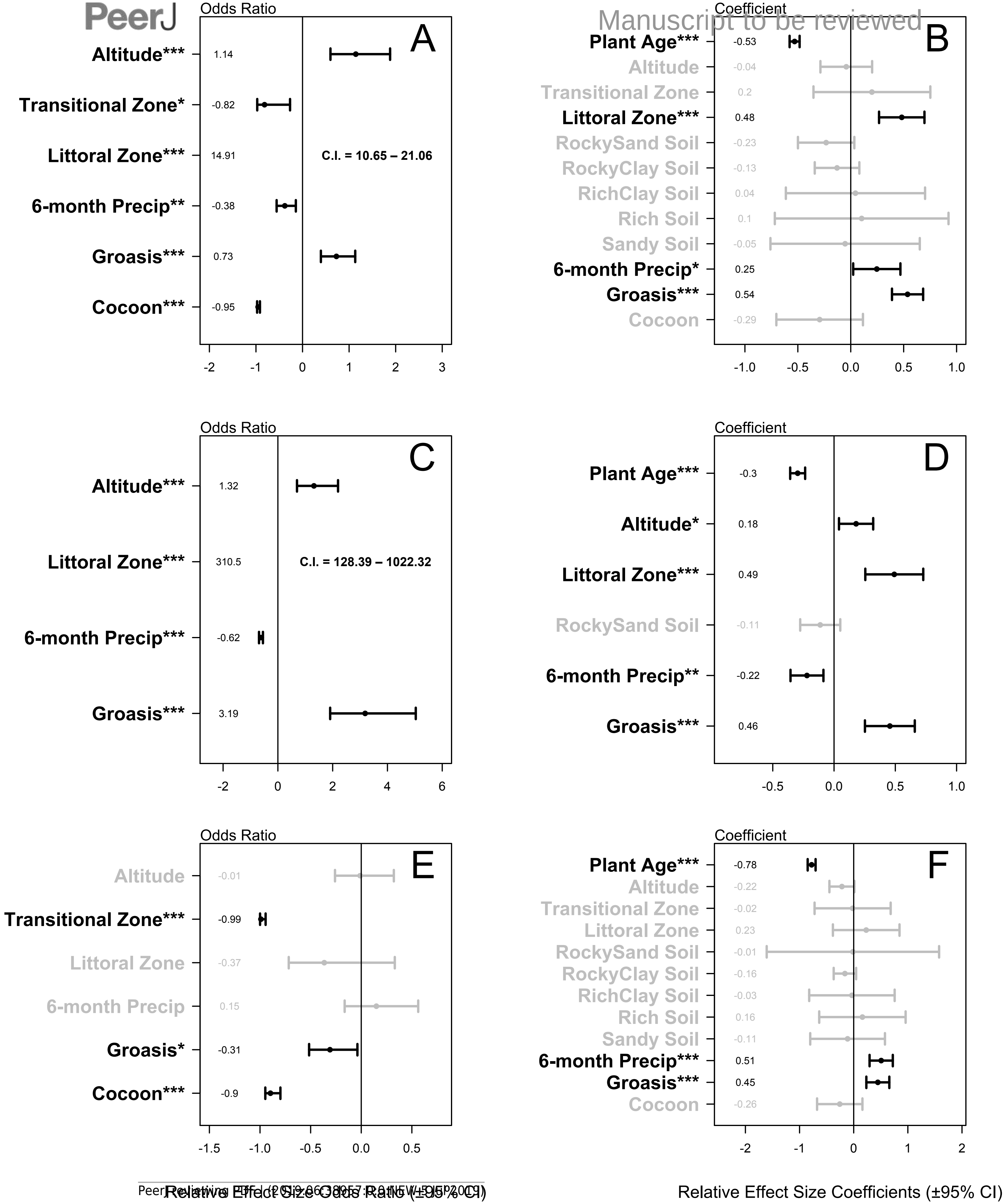

A
B
C
D
Proportion
1.0
0.8
0.6
0.4
0.2
0.0
73.2% dead
26.8% alive
37.8% dead
62.2% alive
33.3% dead
66.7% alive
68.8% dead
31.2% alive
20.3% dead
79.7% alive
55% dead
45% alive
34.5% dead
65.5% alive
22.2% dead
77.8% alive
72.2% dead
27.8% alive
27.3% dead
72.7% alive
control
N = 82
groasis
N = 519
control
N = 3
groasis
N = 16
control
N = 74
cocoon
N = 20
groasis
N = 255
control
N = 9
cocoon
N = 18
groasis
N = 33
dead
bad
normal
good

Figure 5(on next page)

Plots of the relative effect of variable parameters on two-year survival and growth rate of planted *Opuntia* individuals.

A. all islands two-year survival; B. all islands growth rate; C. Plaza Sur island two-year survival; D. Plaza Sur island growth rate; E. all islands excluding Plaza Sur two-year survival; and F. all islands excluding Plaza Sur growth rate. Each point represents coefficient estimate +/- bootstrapped 95% confidence intervals. P-values are generated based on the Satterthwaite method (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$). Values for two-year survival models are converted to odds ratio by exponentiating coefficients and subtracting one. Analyses are based on data from Baltra, Floreana, Plaza Sur, and Santa Cruz islands. Littoral zone values in A. and C. fall outside the scale of those boxes, so confidence intervals are presented as text.


A
Odds Ratio
Altitude*** 1.14
Transitional Zone* -0.82
Littoral Zone*** 14.91
C.I. = 10.65 – 21.06
6-month Precip** -0.38
Groasis*** 0.73
Cocoon*** -0.95
-2 -1 0 1 2 3
B
Coefficient
Plant Age*** -0.53
Altitude -0.04
Transitional Zone 0.2
Littoral Zone*** 0.48
RockySand Soil -0.23
RockyClay Soil -0.13
RichClay Soil 0.04
Rich Soil 0.1
Sandy Soil -0.05
6-month Precip* 0.25
Groasis*** 0.54
Cocoon -0.29
-1.0 -0.5 0.0 0.5 1.0
C
Odds Ratio
Altitude*** 1.32
Littoral Zone*** 310.5
C.I. = 128.39 – 1022.32
6-month Precip*** -0.62
Groasis*** 3.19
-2 0 2 4 6
D
Coefficient
Plant Age*** -0.3
Altitude* 0.18
Littoral Zone*** 0.49
RockySand Soil -0.11
6-month Precip** -0.22
Groasis*** 0.46
-0.5 0.0 0.5 1.0
E
Odds Ratio
Altitude -0.01
Transitional Zone*** -0.99
Littoral Zone -0.37
6-month Precip 0.15
Groasis* -0.31
Cocoon*** -0.9
-1.5 -1.0 -0.5 0.0 0.5
F
Coefficient
Plant Age*** -0.78
Altitude -0.22
Transitional Zone -0.02
Littoral Zone 0.23
RockySand Soil -0.01
RockyClay Soil -0.16
RichClay Soil -0.03
Rich Soil 0.16
Sandy Soil -0.11
6-month Precip*** 0.51
Groasis*** 0.45
Cocoon -0.26
-2 -1 0 1 2
Relative Effect Size Odds Ratio (±95% CI)
Relative Effect Size Coefficients (±95% CI)